Habitat selection by feral cats and dingoes in a semi-arid woodland environment in central Australia

G. P. EDWARDS,1* N. DE PREU,2 I. V. CREALY1 AND B. J. SHAKESHAFT1

1Parks and Wildlife Commission of the Northern Territory, PO Box 1046, Alice Springs, Northern Territory 0871, Australia (Email: glen.edwards@nt.gov.au) and 2Department of Environment and Heritage, Hawker, South Australia, Australia

Abstract  Habitat use by feral cats and dingoes was examined within a heterogeneous semi-arid woodland site in central Australia over 2 years. Density estimates of feral cats based on tracks were higher in mulga habitat than in open habitat. Isodar analysis implied that this pattern of habitat use by feral cats was consistent with the consumer-resource model of density-dependent habitat selection, which is an ideal free solution. The reason why mulga supported higher densities of feral cats was unclear. Foraging success of feral cats may be higher in the mulga because the stalk and ambush hunting tactics typically employed by felids are well suited to dense cover. Mulga may also have offered feral cats more protection from dingo predation. Dingo activity was distributed uniformly across habitats. The dingo isodar was statistically non-significant, suggesting that habitat selection by dingoes was independent of density.

Key words: density-dependent habitat selection, dingo, dispersion, feral cat, habitat, isodar analysis.

INTRODUCTION

In this study we examined habitat use by feral cats (Felis catus) and dingoes (Canis lupus dingo) within a heterogeneous semi-arid woodland site in central Australia. Although differential use of habitats has been shown in both dingoes (Thomson 1992) and feral cats (Konecny 1987; Alterio et al. 1998), no study has examined the possible reasons underlying these phenomena.

Habitat use in animals has been much studied over the past 75 years (Rosenzweig 1991). From early on it was recognized that within some species, individuals actually choose which habitat to occupy and the range of habitats occupied often increases with population density (Mayr 1926; Svärdson 1949; Morisita 1952). This phenomenon is known as density-dependent habitat selection. It appears to be a key factor underpinning patterns of habitat use in animals: food availability, foraging success and competition. The original concept of the ideal free distribution assumed continuous resource input and instantaneous consumption with organisms equilibrating their fitnesses by distributing themselves among the available habitats in proportion to the resources available in those habitats (Fretwell & Lucas 1970; Rosenzweig 1991). The ideal free distribution based on continuous input is the simplest mathematical model of density-dependent habitat selection (Rosenzweig 1991). There are other models, including ideal free models based on discontinuous input (Morris 1994). Isodars, which are regressions of density between two habitats, can discriminate between the various models of habitat selection (Morris 1988, 1994). Isodars have been used to identify possible mechanisms underlying habitat selection and population regulation in rodents (Morris 1987, 1988, 1989, 1992, 1994; Abramsky et al. 1997). The present study is the first to apply a similar habitat analysis to mammalian carnivores.

Another factor that can influence habitat selection in animals is predation (Lima & Dill 1990). A large number of studies have shown that in the presence of a predator, prey species select protected habitats or areas within habitats where the threat of predation is diminished (e.g. Kotler 1984; Carey 1985; Gilliam & Fraser 1987; Hughes et al. 1994). For the simple case where predation risk is constant within a habitat, predation can be viewed as part of the cost of habitat use.
in much the same way as food availability and is already accommodated in models of density-dependent habitat selection such as the ideal free distribution and its derivatives (Rosenzweig 1991). Sometimes, however, the influence of predation on habitat selection is more complex. A range of foraging animals including birds (Lima 1985) and mammals (Lima et al. 1985; Brown 1988; Kotler et al. 1991) demonstrate a clear predation–energy trade-off where the distance from refuge or amount of illumination influences the time spent in risky habitats. In the present study we considered the effects of dingo density on habitat use by feral cats, as dingoes are a potential predator and competitor of cats (Corbett 1995).

**METHODS**

**Study site**

The study site in the Northern Territory, approximately 110 km north-west of Alice Springs, was approximately 550 km² in area and has been described in detail in Edwards et al. (2000). In brief, it is dominated by a flat plain that is elevated at 650 m a.s.l. The plain comprises two land systems (= habitats) with different vegetation. The Hamilton land system has texture contrast soils, some red earths and red clay soils that support a mosaic of open grassland dominated by wiregrass (*Aristida contorta*) and open mixed woodland with scattered mulga (*Acacia aneura*), ironwood (*Acacia estrophiolata*), witchetty bush (*Acacia kempeana*), whitewood (*Atalaya hemiglauca*) and bloodwood (*Corymbia opaca*). The Bushy Park land system is flanked by the Hamilton land system (Perry et al. 1962). It has red earths, which support open to dense stands of mulga woodland with scattered ironwood, witchetty bush and bloodwood over grassland with shrubs (mainly *Eremophila* spp.). Hereafter we refer to these land systems, respectively, as ‘open’ habitat and ‘mulga’ habitat. Dingoes and feral cats occur throughout the study area but red foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*) are rare or absent (Edwards et al. 2000). Cattle (*Bos taurus*) are grazed throughout the study site.

**Track monitoring**

The tracks of feral cats and dingoes were counted to assess populations of these species on nine occasions at approximately 3-month intervals starting in August 1995 and finishing in August 1997. Tracks were counted along two 25-km stretches of dirt road (= transects) in the eastern and western sections of the study site. The roads had a sandy surface substrate that allowed recording of tracks and other signs of animals and provided broad coverage of the study site. During each survey period, tracks were counted along each transect every day for 3 consecutive days. Twenty-four hours before the first count of a survey period, each transect was cleared by towing a 1.8-m long heavy steel bar behind a four-wheel-drive vehicle to erase all previous tracks and signs. Track counts were conducted during the following morning by two observers driving all-terrain vehicles at average speeds of 5–8 km h⁻¹, each observer counting along one transect. Track counts commenced approximately 0.5 h after sunrise and were completed within 3.5 h.

Each time that new feral cat or dingo tracks were detected during a count they were closely inspected and identified to species. The following data were also recorded for each new set of tracks: (i) the distance of the tracks from the start point; (ii) the distance that the tracks remained on the road; (iii) the behaviour of the animal (whether it walked along the road or simply walked across the road); (iv) whether the prints were made by a small or large animal; (v) whether one or more animals had made the tracks; and (vi) the habitat in which the tracks were observed. The road was prepared for the next day’s count by towing a 1.2-m length of steel as before.

**Habitat assessment**

The proportion of the study site occupied by each habitat was determined by assessing the relative incidence or ‘cover’ of each habitat along each of the two transects. These were formally surveyed in July 1997 using a modification of the line intercept technique (Mueller-Dombois & Ellenberg 1974). Habitat observations were made by an observer in the passenger seat of a four-wheel-drive vehicle driven at 20 km h⁻¹ with the vehicle odometer being used to record habitat intercept distances to the nearest 100 m.

**Data analysis**

A problem with track-based surveys of population abundance for territorial species such as feral cats (Corbett 1979) and dingoes (Thomson 1992) is that the total number of tracks of a particular species encountered is likely to be a function of activity levels of individuals in the population as well as population density (Edwards et al. 2000). To overcome this problem, for feral cats we estimated density from the minimum number of animals responsible for observed tracks. Minimum numbers were estimated according to the following criteria. Feral cat tracks separated by 500 m were attributed to one individual. The
500 m classification criterion was based on knowledge of the size of the daily home range of feral cats in the study area (core area of approximately 20 ha: Edwards et al. 2001). A distance of 500 m was also used by Mahon et al. (1998) to classify individual feral cat tracks in a similar study.

Dingoes are much more mobile than feral cats; individual dingoes have been shown to travel up to 20 km in just 7.5 h (Corbett 1995). Also, dingoes in arid areas have much larger long-term home ranges than feral cats (dingoes 37–160 km²; Thomson 1992; feral cats 1.7–22 km²: Jones & Coman 1982; Edwards et al. 2001). As the spatial scale of the habitat patches (see Results section) was small in relation to dingo movements, it was neither practical nor appropriate to assess dingo density in each habitat in the manner described previously for feral cats. Rather, to gauge the relative use of habitats by dingoes we viewed our 25-km transects as being 25 contiguous 1-km cells and tallied the number of cells in each habitat that registered dingo tracks. In cases where a cell containing both habitats registered dingo tracks, both habitats were deemed to have registered tracks. We summed our estimates of the number of ‘individual’ cats and cells with dingo tracks observed across days and transects for each habitat within survey periods. We then divided the total number of cells with dingo tracks for each habitat by the relative area covered by that registered dingo tracks. In cases where a cell containing both habitats registered dingo tracks, both habitats were deemed to have registered tracks. We summed our estimates of the number of ‘individual’ cats and cells with dingo tracks observed across days and transects for each habitat within survey periods. We then divided the total number of cells with dingo tracks for each habitat by the relative area covered by the respective habitats within the study site to give an estimate of the relative ‘density’ of each species for each habitat. For dingoes in particular, this measure is similar to the ‘activity density’ measure used by Abramsky and Pinshow (1989) and Abramsky et al. (1991, 1997), which is also based on tracks.

The dispersion of feral cats and dingoes in relation to habitat was analysed with \( \chi^2 \) goodness of fit. A heterogeneity \( \chi^2 \) analysis was performed initially on uncorrected data to test whether pooling of data across sampling periods was justified (Zar 1996). Pooling can improve statistical power (Zar 1996). Where pooling was justified, the Yates correction for continuity was used to overcome the discrete distribution problem with \( \chi^2 \) values based on single degrees of freedom (Zar 1996). Isodars were constructed to determine whether the patterns of habitat use by feral cats and dingoes fitted any of the currently proposed models of density-dependent habitat selection: continuous input (ideal free), consumer-resource (ideal free) and preemptive (Morris 1994). Isodars were constructed using central trend lines based on geometric mean regression following Krebs (1999), as both the \( x \) and \( y \) variables had measurement error. In cases where isodars were linear on an arithmetic scale and had zero intercepts, the data were logarithmically transformed to test whether logarithmic solutions were better than arithmetic ones (Morris 1994). Pearson correlation analysis was used to examine whether the relative density of feral cats in a particular habitat was related to the density of dingoes in that habitat or with dingo abundance across the study site (habitats pooled). The total number of cells with dingo tracks was used as the latter measure in the correlations. Correlation analyses were performed using SYSTAT 8.02 (SYSTAT Inc., Evanston, Illinois, USA).

RESULTS

The cover data pooled between the transects showed that the study site had 36% mulga habitat and 64% open habitat. The two habitats tended not to be interspersed in a fine-scale matrix but rather occurred as large patches greater than 10 km² in size. Aerial photographs of the study site supported this interpretation. The habitat proportions did not change during the study, thereby satisfying the independence from landscape assumption (Morris 1994). This precluded having to use weighted means of habitat supply in the isodar analyses.

Heterogeneity \( \chi^2 \) analysis of the cat and dingo track data indicated that pooling of data between sample periods was justified (cats: \( \chi^2 = 8.7, 0.25 < P < 0.50 \); dingoes: \( \chi^2 = 7.8, 0.25 < P < 0.50 \)). The pooled tests with Yates correction showed that dingoes were distributed uniformly across habitats (\( \chi^2 = 0.3, 0.50 < P < 0.75 \)) but feral cats were not (\( \chi^2 = 20.7, P < 0.001 \)). Relative density of feral cats was higher in mulga than in open habitat.

For feral cats, the arithmetic isodar solution was
implied that the two habitats differed quantitatively are renewed (Morris 1994). The non-zero intercept are incapable of consuming resources as quickly as they are renewed (Morris 1994). This is an ideal free solution where individuals resource model of habitat selection (Morris 1988, regulation (Morris 1988) consistent with the consumer-resource model. At our study site, resources are unlikely to be renewed at a constant rate given the vagaries of arid ecosystems (Noy-Meir 1973; Caughley 1987) nor consumed by feral cats as soon as they are renewed given that: (i) feral cats occur at relatively low densities at the study site (Edwards et al. 2000, 2001); and (ii) the day-to-day movements of feral cats occur over a relatively large spatial scale (Edwards et al. 2001). The feral cat isodar indicates that there are initial differences in reproductive rewards between the mulga and open habitats, the former having the higher reward through the eyes of the feral cats. At very low densities, only mulga should be occupied by feral cats until increased density reduces the fitness rewards in mulga to those initially available in the open (Morris 1988). Thereafter, as density increases, an equal number of individuals is added to each of the habitats (= parallel regulation: Morris 1988). However, the difference in density between the habitats will fall as the overall population density increases. With parallel regulation, density-dependent feedback on reproductive fitness is linear and alike in both habitats (Morris 1988). Parallel regulation is consistent with the notion that dispersal from high density (source) to low

**DISCUSSION**

Chi-squared analyses indicated that feral cats were consistently more abundant in mulga than in open habitat at our study site. The isodar solution supported this result. This is within expectations because preferential use of cover has been widely reported in the Felidae. Scottish wildcats (*Felis silvestris*) were found to favour dense pine forests and scrub (Corbett 1979), *F. rufus* on the Galápagos Islands were found more often in lava/shrub habitat than in open habitats (Konecny 1987), *F. catus* in New Zealand were attracted to vegetation buffers surrounding open habitat (Alterio et al. 1998), pumas (*Puma concolor*) were found to use mixed swamp and hammock forests preferentially, which provided more cover than other habitats (Belden et al. 1988), and bobcats (*F. rufus*) were found to use habitats with dense understorey more than open habitats (Progulske 1982, cited in Wassmer et al. 1988).

The linear signature of the feral cat isodar on the arithmetic scale implied density-dependent population regulation (Morris 1988) consistent with the consumer-resource model of habitat selection (Morris 1988, 1994). This is an ideal free solution where individuals are incapable of consuming resources as quickly as they are renewed (Morris 1994). The non-zero intercept implied that the two habitats differed quantitatively rather than qualitatively (Morris 1988). Qualitative differences between habitats may include differences in structure or in the kinds of resources or kinds of interacting species that they contain (Morris 1988). Quantitative differences are differences in the availability or richness of resources such as food and shelter (Morris 1988).

It is intuitively appealing that habitat selection by feral cats appears consistent with the consumer-resource model. At our study site, resources are unlikely to be renewed at a constant rate given the vagaries of arid ecosystems (Noy-Meir 1973; Caughley 1987) nor consumed by feral cats as soon as they are renewed given that: (i) feral cats occur at relatively low densities at the study site (Edwards et al. 2000, 2001); and (ii) the day-to-day movements of feral cats occur over a relatively large spatial scale (Edwards et al. 2001). The feral cat isodar indicates that there are initial differences in reproductive rewards between the mulga and open habitats, the former having the higher reward through the eyes of the feral cats. At very low densities, only mulga should be occupied by feral cats until increased density reduces the fitness rewards in mulga to those initially available in the open (Morris 1988). Thereafter, as density increases, an equal number of individuals is added to each of the habitats (= parallel regulation: Morris 1988). However, the difference in density between the habitats will fall as the overall population density increases. With parallel regulation, density-dependent feedback on reproductive fitness is linear and alike in both habitats (Morris 1988). Parallel regulation is consistent with the notion that dispersal from high density (source) to low

**Fig. 2.** Arithmetic relationship between the activity of dingoes in open and mulga habitats in central Australia. Relative activity is the total number of 1-km cells with dingo tracks for each habitat divided by the relative area covered by each habitat within the study site.
density (sink) habitats is an important population regulation mechanism (Morris 1988 and others therein).

It is interesting to consider why feral cats at our study site were more abundant in mulga habitat than open habitat. In central Australia, small mammals are the most important prey of feral cats, but birds, reptiles and invertebrates are also eaten (Paltridge et al. 1997). Three-monthly monitoring of feral cat prey species at our study site indicated that small mammal species’ composition and abundance were often similar across habitats. However, there were marked differences in the bird and reptile faunas in each habitat and both birds and reptiles were more abundant in the open habitat (G. P. Edwards & N. de Preu, unpubl. data, 1994–1997). This implies that the open habitat was in fact richer in food resources than was mulga. However, some prey are more susceptible to cat predation than others (Paltridge et al. 1997) and the apparent irregularity between total prey abundance and habitat use by feral cats may be due to a lack of correlation between total prey abundance and available prey. An additional point to consider in this regard is that the stalk and ambush hunting tactics typically employed by felids are well suited to dense cover (Murray et al. 1995), which is typical of mulga habitat. This may confer greater foraging success in mulga than in the open, thereby making mulga the more productive habitat.

Although habitat selection in feral cats was not related to changes in dingo activity, this does not mean that predation risk was not important. For feral cats, the risk of predation by dingoes may have been similar between habitats or the mere presence of just one dingo may have been enough to influence feral cats to choose the habitat richer in protective cover (i.e. mulga habitat).

The results of this study suggest that in conservation programs where an objective is to mitigate predation by feral cats, habitats affording cover are prime locations for the placement of poison baits and/or traps targeting the species. The χ² analyses indicated that dingoes showed a preference for neither mulga nor open habitat. The statistical non-significance of the dingo isodar regression suggested that habitat selection by dingoes was density independent (Morris 1988), at least at the scale considered. At a dissimilar site in north-western Australia, the use of habitats by radio-collared dingoes was disproportionate to availability: riverine areas were used much more intensively than floodplains, hills or stony habitats (Thomson 1992). The observed pattern of habitat use in the north-western Australian study is not necessarily incongruous with the findings of the present investigation. Isodar analysis was not performed in the north-western Australian study and distribution data alone tell us little about mechanisms underlying habitat use (Morris 1994). If the riverine habitat were qualitatively and/or quantitatively superior to the other habitats, dingoes should have favoured the riverine habitat irrespective of whether density-dependent or density-independent factors were at play.

ACKNOWLEDGEMENTS

This study was jointly funded by the Parks and Wildlife Commission of the Northern Territory and Environment Australia (formerly the Australian Nature Conservation Agency). The study was approved by the Alice Springs Animal Ethics Committee. We thank the many volunteers who assisted with field work, particularly Jok Markham. Ken Johnson, Dave Lawson, Bill Freeland, Catherine Meathrel and Doug Morris in particular provided useful comments on drafts of this paper. We also thank the owners and managers for allowing us to work on Hamilton Downs Station.

REFERENCES


Habitat selection in feral cats and dingoes


